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Large river floodplain as a natural laboratory: non-native macroinvertebrates benefit from elevated temperatures

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Abstract. Water temperature is known to influence individual animal metabolism, development, and reproduction. However, in situ studies aiming to demonstrate the link between water temperature and community structure in complex ecosystems such as large river floodplains are still rare. In particular, we have little indication about how an increase in temperature affects the density of native and invasive species within a community. Large river floodplains cover a varied range of environmental conditions, are rich in species, and therefore potentially useful ecosystems to study the effect of water temperature at the community level. Moreover, as freshwater communities are increasingly impacted by global warming and biological invasions, an improved understanding of the possible interaction between these drivers would be beneficial. First, we studied during two years the thermal heterogeneity of 36 sites in a large river (Rhone) floodplain. Second, we compared the thermal regimes of sites having different levels of hydrological connectivity with the main river channel. Third, we studied the combined and separated effects of the thermal regime and the hydrological connectivity on the presence and densities of native and non-native species of macroinvertebrates. The studied large river floodplain covered a wide range of thermal regimes, with some sites displaying a yearlong constant temperature of about 10°C, whereas others experienced thermal amplitude of over 25°C. The thermal regime was independent of the level of hydrological connectivity of the sites. The increase in hydrological connectivity had a significant and positive effect on the richness of non-native species within sites. The thermal regime had a positive influence on the density of non-native species but no effect on the total density of native taxa within communities. This study showed that large river floodplains possess a wide range of thermal conditions and that the increase in water temperature can have a positive influence on the presence of non-native populations of macroinvertebrates. This study provides a first set of empirical results to establish models predicting the effect of increasing temperatures on the establishment of non-native and native species in a complex ecosystem and underline the problem of biological invasions under climate change.

Key words: air–water temperature; alien species; biological invasions; climatic change; ecosystem management; generalized additive models; lateral connectivity; Rhone River; species distribution model; thermal pollution.

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Introduction

Temperature can have a profound effect on the growth, development, and metabolism of organisms (Brown et al. 2004). In a world experiencing global change, both the composition and abundance of communities can be expected to change in freshwater environments that are especially vulnerable to compounded effects of climate warming and biological invasions (Sala et al. 2000, Rahel and Olden 2008). For instance, Milner et al. (2001) showed in glacier-fed streams that the composition of macroinvertebrates changed when water temperature increased by two degrees. Likewise, Castella et al. (2001) showed that the maximum water temperature in a glacier-fed stream was an explanatory variable for changes in macroinvertebrate composition. Fish abundance has also been shown to be related to flow and temperature conditions in the lower part of the Rhone River, with higher abundance in warm habitats (Daufresne et al. 2004).

Increasing temperatures have been shown to especially favor the spread and establishment of non-native species (e.g., Domisch et al. 2013, Gallardo and Aldridge 2013*a*), which may be better suited to thermal changes than are native taxa. Non-native species can be a major threat to biodiversity and continue to proliferate at an increasing rate (Chapin et al. 2000, Sala et al. 2000). In freshwater systems, warmer temperatures have been shown to facilitate the spread of invasive species at both the continental and within-catchment scales. For instance, Gallardo and Aldridge (2013*a*) showed that the spread of Ponto-Caspian invaders into western Europe was highly correlated with elevated temperatures, while Verbrugge et al. (2012) demonstrated that non-native mollusks in the Rhine River tend to tolerate warmer habitats than native species. Native aquatic macroinvertebrates are highly vulnerable to the negative effects of invasive species, which often display strong competitive abilities (Statzner et al. 2008, DAISIE 2009).

To date, studies have mostly focussed on the effects of climate change and invasive species on the communities within the main channel of rivers (e.g., Daufresne et al. 2004). However, large river floodplains provide an ideal and important system for exploring the effects of invasive species as they cover a wide range of thermal conditions (Tonolla et al. 2010), and support rich aquatic macroinvertebrate communities which themselves display multiple strategies to adapt to extreme conditions (Statzner et al. 2001, Verberk et al. 2008).

In large river floodplains, the lateral, vertical, longitudinal, and temporal dimensions provide a wide diversity of habitat conditions (Gray and Harding 2009). Water temperature varies temporally due to seasonal changes in air temperature and melting snow in spring (Tonolla et al. 2010) and longitudinally in the main river channel with colder water in the highlands compared to the lowlands. Groundwater-fed channels with a high vertical connectivity have a more constant surface temperature than channels with low vertical connectivity (Caissie 2006). In the lateral dimension of floodplains, channels can be permanently connected to the main river channel, partially or totally disconnected (Amoros and Bornette 2002). This gradient of lateral hydrological connectivity can generate differences in water temperature of 16°C (Ward et al. 2001, Webb et al. 2008) and has been shown to influence the distribution of animal communities (Reckendorfer et al. 2006, Lasne et al. 2007). The link between water temperature and lateral hydrological connectivity is, however, poorly studied in large river floodplains. This is due primarily to the challenges in undertaking the long-term temperature monitoring necessary to develop a clear understanding of spatial and temporal patterns.

While temperature is believed to influence non-native species distribution and is commonly used to model their potential range of establishment (Domisch et al. 2013, Gallardo and Aldridge 2013*a*), very few studies have examined the impact of temperature on the distribution of non-natives in situ. An existing study by Verbrugge et al. (2012), however, showed that non-native mollusks in the Rhine River tend to tolerate warmer habitats than native species. As such, it is possible that water temperature is an important factor influencing the success of non-native populations in floodplain channels, and this topic is worthy of further investigation. A better understanding of the influence of water temperature on the establishment of non-native species in river floodplains can have implication for ecosystem management, biological conservation and to

forecast the effect of global warming on the spread of aquatic non-native species.

The aims of our current research were (1) to measure the thermal regime of the Rhone River and its floodplain, (2) to differentiate the effects of water temperature and hydrological connectivity on macroinvertebrates, and (3) to model the effect of water temperature on native and non-native macroinvertebrate abundance and richness. We hypothesized that floodplain channels would encompass a large diversity of thermal regimes independently from their level of lateral hydrological connectivity with the main river channel. We also hypothesized that the hydrological connectivity of a site would influence macroinvertebrate composition and richness such as described in previous studies (Reckendorfer et al. 2006, Paillex et al. 2015), while water temperature would influence the abundance of the species (e.g., Verbrugge et al. 2012). Finally, we hypothesized that native and non-native taxa would respond differently to water temperature and in particular that higher water temperature would encourage non-native species.

Materials and Methods

Measurements of temperature

The study was carried out in two sectors of the French Rhone River (i.e., Belley and Brégnier Cordon; Fig. 1). Thirty-seven data loggers (Onset HOBO data loggers) were installed in the Rhone River and its floodplain to record hourly water temperature. Temperature loggers were installed in different habitats (i.e., lotic or lentic sites) to cover the thermal diversity that exists in the floodplain. Four loggers were installed in the main river channel (Fig. 1). In addition to these four loggers, the data of two permanent stations in Belley and Brégnier-Cordon measured by Compagnie Nationale du Rhône (CNR; authority managing the Rhone River) were used to represent the conditions in the main river channel (Fig. 1). Five loggers were installed in secondary floodplain channels permanently connected with the main river channel (i.e., eupotamal channels; Fig. 1; Appendix S1: Fig. S1). Eleven were installed in secondary channels with a permanent connection downstream with the main river channel (i.e., parapotamal channels; Fig. 1; Appendix S1: Fig. S1). Fifteen were installed in disconnected channels that are in direct connection with the main river only during floods (i.e., plesiopotamal channels; Fig. 1; Appendix S1: Fig. S1). Two loggers were installed, respectively, in Belley and Brégnier-Cordon sectors to measure air temperature (Fig. 1). All loggers recorded the water and air temperature hourly in °C with an error of ±0.2°C, from the 1 January 2009 to 31 December 2010.

Lateral connectivity gradient

As described in Paillex et al. (2007), we summarized with a principal component analysis (PCA) five environmental variables known to represent the level of lateral hydrological connectivity in a given channel. The five variables (submerged vegetation cover, organic matter in the upper part of sediments, water conductivity, diversity of the mineral grain size measured by a Simpson index, and water NH_3-N) were measured during the same years as the monitoring of temperature and the macroinvertebrate samplings. The organic content of the sediment and the water concentration of NH_3-N were measured during the winter period. The cover of submerged vegetation, the diversity of mineral grain size, and conductivity were measured during macroinvertebrate samplings. The first axis of the PCA summarized the level of lateral connectivity for each site (Paillex et al. 2007). This ordination of the sites has the advantage of providing a value of lateral connectivity for each site, avoiding classification of the sites into discrete categories. This surrogate of lateral connectivity was shown to be well correlated with common hydrological indices (i.e., upstream overflow frequency and magnitude, and shear stress during floods, see Riquier et al. 2015).

Thermal variables and gradient

In order to describe the heterogeneity of thermal regimes among channels, we studied the relationship between water and air temperature in the main river and floodplain channels. The relationships were analyzed with logistic regressions. The best model was selected as having the smallest Akaike's information criterion (AIC; Mohseni et al. 1998, Ritz and Streibig 2005). The relationship between water and air temperature has already been modeled for rivers (Koch and Gruenewald 2010) and has been proved useful in characterizing their thermal regimes (Morrill

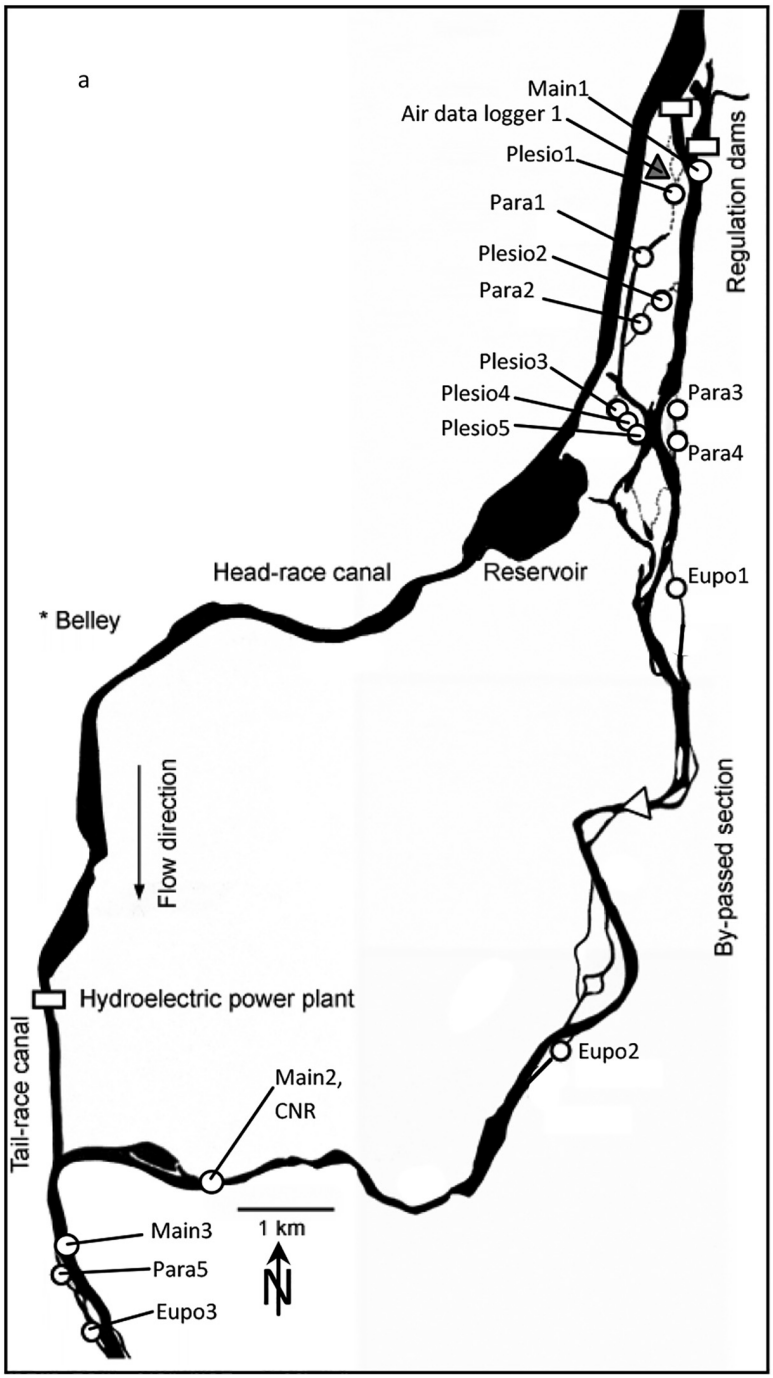
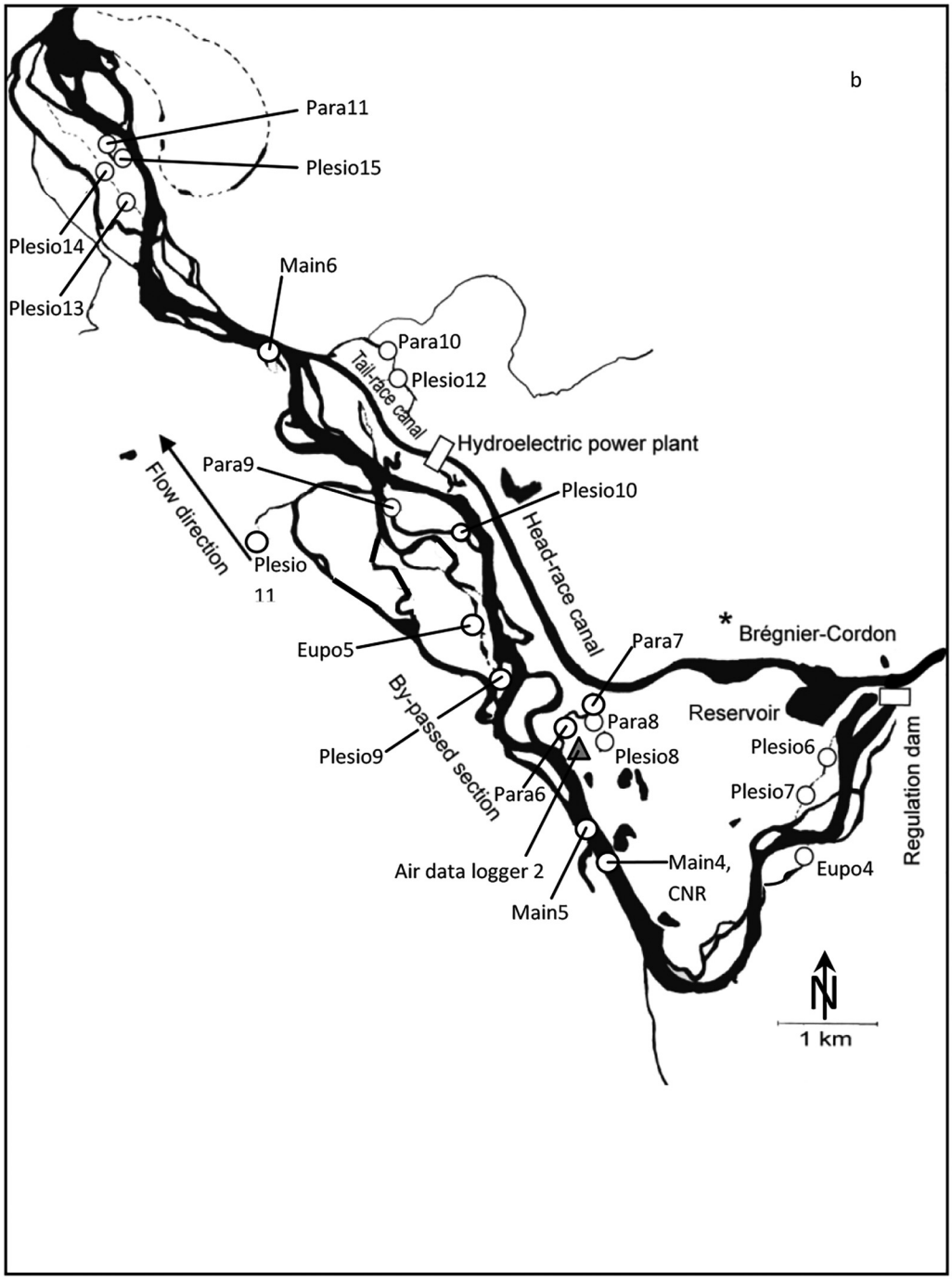


Fig. 1. Locations of sampling sites in Belley (a) and Brégnier-Cordon (b) sectors. The sites are coded according to their type of connection with the main river channel: main river channel (Main), permanently connected channels called eupotamal channels (Eupo), upstream disconnected channels called parapotamal channels (Para), upstream and downstream disconnected channels called plesiopotamal channels (Plesio), and numbered for each category along the flow direction in the two studied sectors (Main: 1–6, Eupo: 1–5, Para: 1–11, Plesio: 1–15). Triangles represent data loggers measuring air temperature.



(Fig. 1. *Continued*)

et al. 2005). Logistic regressions were used to derive parameters that can be used to characterize the thermal regimes (see Appendix S1: Table S1). The following three parameters derived from the relationship between air and water temperatures were found to best describe the thermal regime: (1) the asymptotic maximum (as_max), (2) the inflexion point (infl), and (3) the

slope of logistic regressions (slope; see Appendix S1: Table S1). The asymptotic maximum reflects the maximum water temperature even if the air temperature continues to increase. The inflexion point reflects the air temperature at which water temperature changes from an increasing to a decreasing trend or vice versa. The slope reflects the speed of temperature increase. The efficiency of the logistic regressions was tested by Nash–Sutcliffe efficiency tests (NSE). Nash–Sutcliffe efficiency ranks between 0 and 1, where 1 is the optimal value (Moriasi et al. 2007). A threshold of 0.70 was selected to discriminate the models correctly fitting with the observations (Moriasi et al. 2007). The root mean square error (RMSE) was also calculated to test the models. It indicates the standard deviation of the prediction error and indicates a better model performance when values are small. The package "drc" (Ritz and Streibig 2005) in R 3.1.0 (R Core Team 2014) was used to calculate and select models. The package "hydroGOF" was used to test the models with NSE and calculate RMSE. In addition, we measured a series of indicators reflecting the thermal regimes of the sites. We measured the maximum and minimum water temperature observed during a year (T_{max} and T_{min}), and the thermal amplitude ($T_{max} - T_{min}$; Appendix S1: Table S1), which reflects the thermal change during a year within a site. The Kamler coefficient was also calculated, which is the ratio of the maximum water temperature divided by the minimum value (T_{max}/T_{min}; Arscott et al. 2001). We calculated the mean water temperature of sites during the studied year (mean_year; Appendix S1: Table S1) and the mean water temperature for each of three seasons: winter (1 January–20 March); spring (21 March–20 June); and summer (21 June–22 September). These eleven variables were selected as they are known to influence macroinvertebrate species occurrence and abundance (Arscott et al. 2001, Daufresne et al. 2004) and included in multivariate analyses to describe the thermal regime of the sites.

Following the same approach of the hydrological gradient, a PCA was performed with the eleven thermal variables to identify composite variables expressing thermal regimes within and among the studied sites (e.g., Vaughan and Ormerod 2005). Site scores along the first PCA axis were used to express a gradient of thermal regime. This approach summarizes the complexity of the data into one unique variable (Vaughan and Ormerod 2005) and permits to test its independence from the gradient of hydrological connectivity. However, the variables can also be analyzed individually to test the specific response of biota, thereby providing a more mechanistic explanation for the distribution of the species. Based on the results of the PCA, Euclidean distances between sites were calculated and sites were classified with a Ward clustering method, which allowed identification of groups of sites with similar thermal regimes. The package "ade4" in R 3.1.0 (R Core Team 2014) was used to perform the PCA, to calculate the Euclidean distances and perform the classification (Chessel et al. 2004). Correlation between the thermal gradient and hydrological gradient was tested with a Spearman rank test, using the "Hmisc" package in R 3.1.0 (R Core Team 2014).

Macroinvertebrate samplings and metrics

Macroinvertebrate communities were sampled in 19 floodplain sites, where water temperature was recorded. Nine sampling sites were sampled in 2009 and 10 in 2010. The macroinvertebrates were sampled in spring and summer to account for seasonal differences and pooled for statistical analyses. In each site, macroinvertebrates were sampled within a quadrat (quadrat size: 0.25 m^2) with a hand net (mesh size: 500 μm) at three random positions along a 15-m stretch. Macroinvertebrates were identified to genus or species level, except Diptera that were identified to family level (see Data S1).

We divided the macroinvertebrates into two groups: the native and the non-native taxa, as they potentially respond differently to the thermal and hydrological gradients (e.g., Townsend et al. 1997, Besacier-Monbertrand et al. 2010, Verbrugge et al. 2012). We tested the effect of hydrological connectivity and temperature gradients on (1) the partition of the variance in taxa abundance, (2) the abundance of communities within sites, and (3) the taxonomic richness of macroinvertebrate communities. Partition of variance for native and non-native assemblages was tested to assess the independent and joint effect of hydrological connectivity and the thermal regime. Individual variables included in the PCA and significantly correlated with the first

axis of the PCA were used to assess the partition of the variance. In addition, the partition of the variance permits the assessment of the residual variability not accounted for by the variables used to explain the faunal data (Peres-Neto et al. 2006). The function varpart from the "vegan" package was used in R (Oksanen et al. 2011, R Core Team 2014). In addition, we tested the response of the macroinvertebrate abundance and richness along the thermal and hydrological gradients for a subgroup of native taxa comprising the Ephemeroptera, Plecoptera, and Trichoptera (EPT), because EPT are known to be favored by a high connectivity of the secondary channels with the main river channel (Usseglio-Polatera and Tachet 1994, Gallardo et al. 2014).

We tested the influence of the environmental variables on the richness and the abundance of macroinvertebrates using generalized additive models (GAMs) with a Poisson link function, a thin plate regression spline as smooth term and a chi-square significance test (Wood 2006). Generalized additive model was chosen instead of other regression procedures because of its ability to deal with nonlinear relationships between the response and the set of explanatory variables (Guisan et al. 2002). When necessary, we used AIC to identify the best model. We used the fitted values of the GAM to plot the relationships between the explanatory and the response variable of the models. Generalized additive model was calculated with the gam function from "mgcv" package (Wood 2006) in R (R Core Team 2014).

Results

Temperatures in the river and floodplain channels

In the floodplains of Belley and Brégnier-Cordon, air temperature oscillated between 0 in winter and 30°C in summer (Fig. 2a for Belley sector). Water temperature recorded in the river and floodplain channels showed contrasting patterns with either a unimodal response similar to the air temperature or a flatter response with little seasonal change (see a selection of examples in Fig. 2 for the year 2009). Water temperatures in the main river and connected channels increased from a minimum around 2.9°C in winter to maximum of 23.4°C in summer (Fig. 2b, c). In contrast, disconnected channels showed a larger variability, with either a more constant yearly temperature and a maximum of 15.5°C in summer (Fig. 2d, e) or larger changes among seasons and a maximum reaching 26.4°C (Fig. 2f).

The water temperature in the main river channel showed an S-shaped relationship with air temperature (Appendix S1: Fig. S2), with an asymptotic minimum and maximum at 3.3°C and 23.4°C, respectively. The minima and maxima were similar among most of the sites in the main river channel (Appendix S1: Fig. S2). However, some disconnected sites experienced a less pronounced S-shaped relationship between the water and air temperatures, with a smaller amplitude (see for example PARA1 in Appendix S1: Fig. S3 and PLES1 in Appendix S1: Fig. S4). Overall, models relating air temperature with water temperature showed good results with NSE > 0.70, with similar patterns between years, and a higher NSE and a lower RMSE when calculated on daily average (Appendix S1: Table S2).

Thermal heterogeneity among sites

The three-first PCA axes obtained with the thermal data from 2009 explained 81.3% of the between-site variability. The first and second axes explained, respectively, 47.5% and 23.4% of the variability. The first axis of the PCA was highly correlated with the yearly maximum water temperature and with the mean summer water temperature, reflecting a gradient of thermal regime from warmer to colder sites (Fig. 3a). A classification of the channels according to their Euclidean distances based on their thermal regimes showed four groups: (1) sites with buffered conditions, (2) sites similar to the main river, (3) sites warmer than the main river, and (4) a group of contrasted sites that did not fit in the previous groups (Fig. 3b; Appendix S1: Fig. S5). The same patterns were observed in 2010 within and among the same floodplain channels. The stability in the ordination between the years was measured as the correlation between site scores along the first (Spearman, $r = 0.83$, $P < 0.001$) and second axes (Spearman, $r = -0.89$, $P < 0.001$).

Hydrological connectivity and thermal regime

The PCA of the lateral connectivity variables ordinated sites from totally disconnected sites (Appendix S1: Fig. S6a, b) to totally connected sites (Appendix S1: Fig. S6a, b). The correlation between the thermal gradient (first PCA axis;

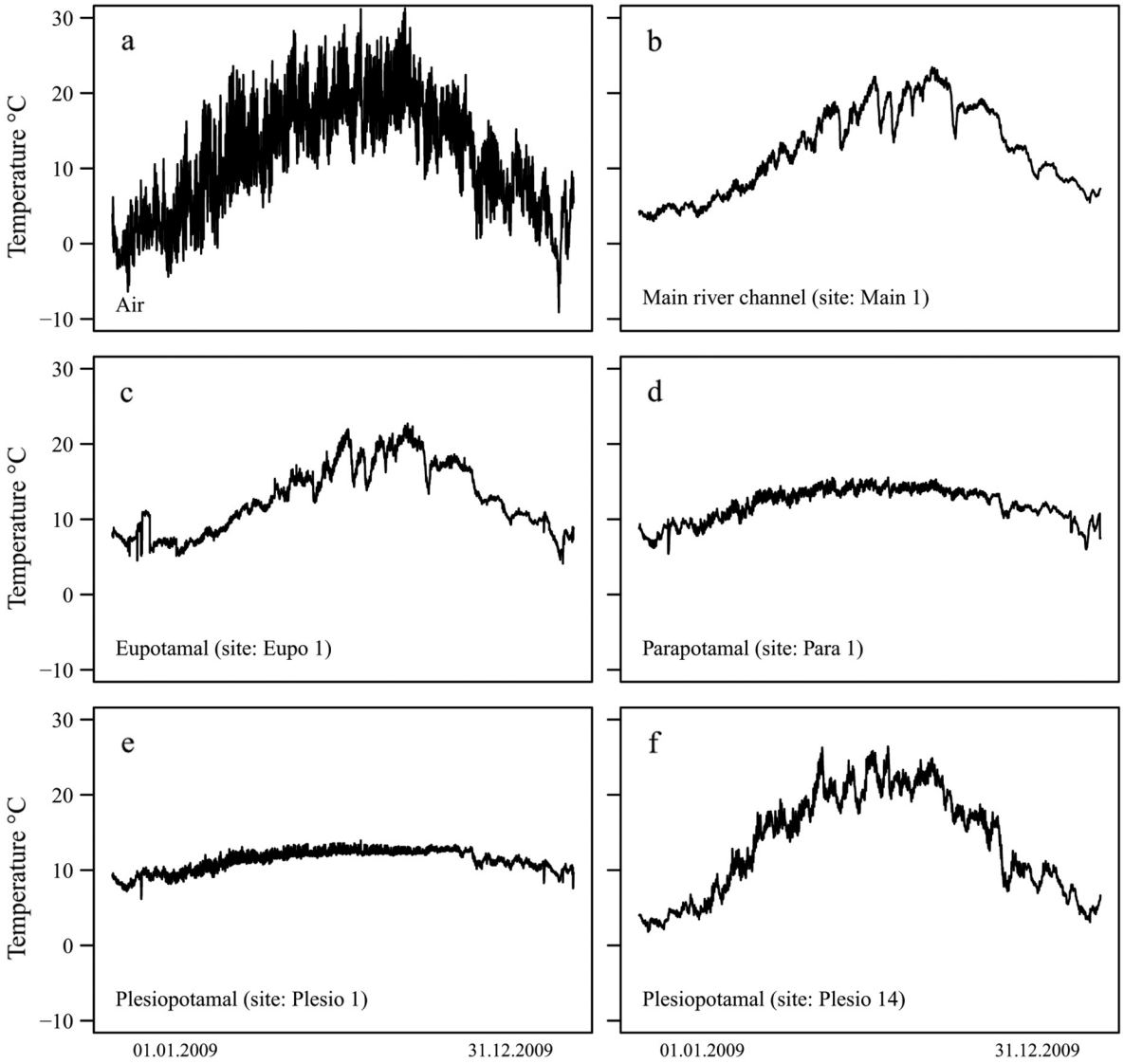


Fig. 2. Hourly air temperature in Belley sector (a) and hourly water temperature in five distinct channels (b–f). Hourly air and water temperatures are represented from the 1st of January 2009 until the end of December 2009. In panel (a), we can observe that the daily fluctuations of air temperature are much larger than for the water temperature in the main river channel (b) and the water temperature in secondary floodplain channels (c–f).

Appendix S1: Fig. S6c) and the gradient of hydrological connectivity (first PCA axis; Appendix S1: Fig. S6a) was not significant (Spearman, $r = -0.35$, $P = 0.11$). The absence of correlation between the two gradients is partially due to the thermal heterogeneity among disconnected channels. Some disconnected sites are warmer in summer whereas others are colder. Moreover, while some disconnected channels had a similar temperature to the main river channel and connected channels in winter (Fig. 2b, f), others had a temperature nearly 5°C higher (e.g., Fig. 2e). Nevertheless, the thermal gradient (first PCA axis; Appendix S1: Fig. S6c) was correlated with the second axis of the gradient of hydrological connectivity driven by water conductivity (Spearman, $r = 0.67$, $P < 0.001$).

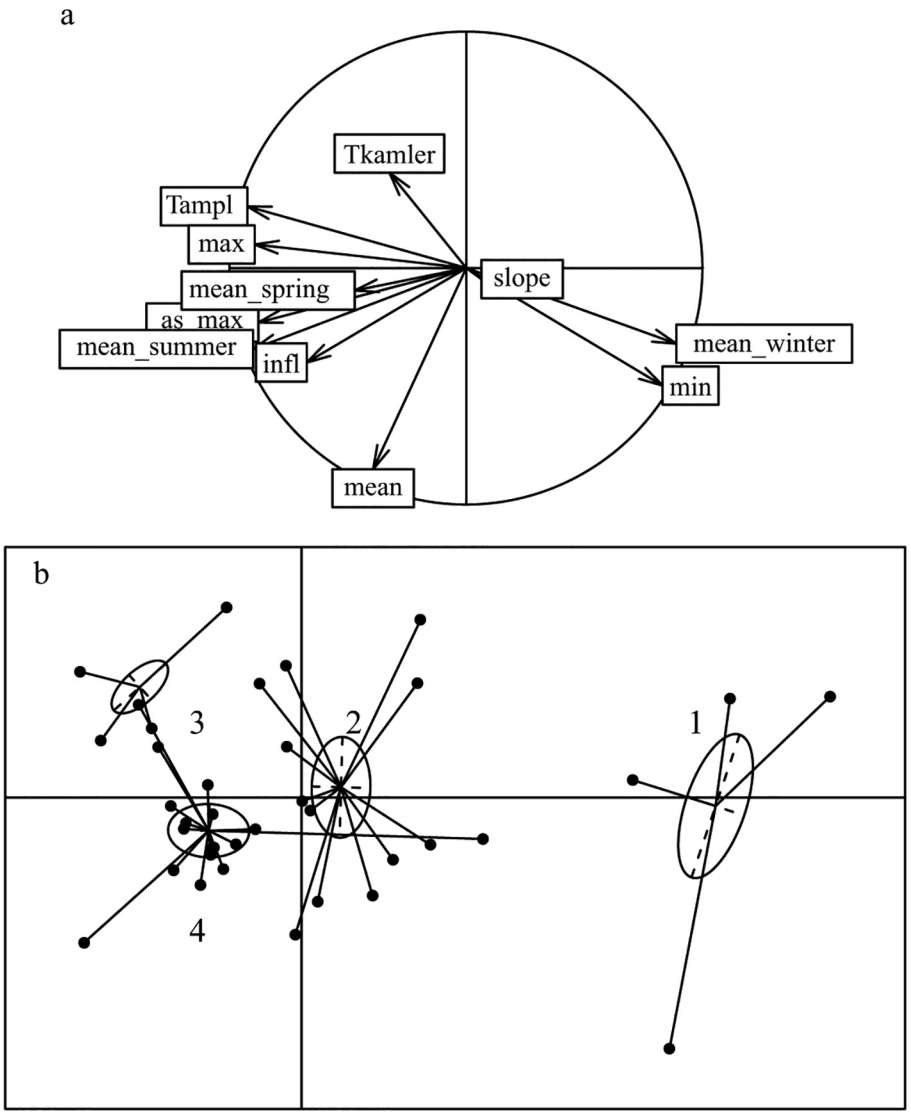


Fig. 3. Principal component analysis based on thermal variables recorded within sites in 2009. (a) Correlation circle of the 11 selected variables. as_max: asymptotic maximum for air–water relationship; infl: inflexion value for air–water relationship; slope: maximum slope for air–water relationship; Tmax: maximum water temperature; Tmin: minimum water temperature; Kamler: TKamler coefficient; Tampl: amplitude; mean: year average temperature; mean_summer: average temperature in summer; mean_spring: average temperature in spring; mean_winter: average temperature in winter. (b) Ordination of the sites according to their thermal regimes and sites grouped according to cluster analysis in Appendix S1: Fig. S5. Group 4 contains sites from the main river channel and eupotamal channels, as well as a few (n = 3) plesiopotamal channels. Group 3 contains sites with a similar thermal regime to sites in group 4. Group 2 contains para and plesiopotamal channels, and group 1 contains sites a different thermal regime from the rest of the sites.

Macroinvertebrate response

One hundred eighty-five native taxa and 12 non-native species were identified in the study area (Table 1). Fifty percent of non-native species were mollusks that colonized up to 65.5% of the sites (see *Physella acuta*; Table 1). Other non-native species present in the study area were arthropods, platyhelminthes, and annelids, and

Table 1. Non-native species observed in 2009 and 2010 in the studied sites.

Species	Phylum	Class	Abundance	No. of invaded sites	Percentage of sites invaded
Corbicula fluminea	Mollusk	Bivalvia	531	11	37.9
Crangonyx pseudogracilis	Arthropoda	Malacostraca	84	10	34.5
Dikerogammarus villosus	Arthropoda	Malacostraca	85	3	10.3
Dreissena polymorpha	Mollusk	Bivalvia	17	7	24.1
Dugesia tigrina	Platyhelminthes	Turbellaria	86	10	34.5
Ferrissia clessiniana	Mollusk	Gasteropoda	40	3	10.3
Gyraulus parvus	Mollusk	Gasteropoda	964	18	62.1
Hemimysis anomala	Arthropoda	Malacostraca	1	1	3.5
Hypania invalida	Annelida	Polychaeta	646	5	17.2
Orconectes limosus	Arthropoda	Malacostraca	3	2	6.9
Physella acuta	Mollusk	Gasteropoda	1748	19	65.5
Potamopyrgus antipodarum	Mollusk	Gasteropoda	3185	17	58.6

Note: Species in boldface are non-native species among the 100 most invasive species in Europe (DAISIE 2009).

found to colonize up to 34.5% of the sites (see *Dugesia tigrina*; Table 1). Three of the observed non-native species are invasive species in Europe, *Corbicula fluminea*, *Dikerogammarus villosus*, and *Dreissena polymorpha* (Table 1). The partition of the variance in the abundance of native taxa was well explained by the thermal regime and the hydrological connectivity (60% of variance explained by both variables combined). The variance was partially explained by the interaction between the thermal regimes and the hydrological connectivity (13%), while 39% was explained by the thermal regime alone (Fig. 4a). Fifty-seven percent of the variance in non-native species abundance was explained by the thermal regime and 29% by the hydrological connectivity (Fig. 4b). For both partitions, the residuals unexplained by the variables represented 40% for native taxa and 31% for non-native species.

In contrast, the richness of macroinvertebrates was generally explained by the hydrological connectivity (Table 2; Appendix S1: Fig. S7). For example, the richness of non-native species was positively related to the gradient of hydrological connectivity (deviance explained 0.51, Table 2; Appendix S1: Fig. S7), and similarly for the richness of EPT taxa (deviance explained 0.79, Table 2; Appendix S1: Fig. S7). While the thermal regime did not explain the richness of non-native macroinvertebrates (Table 2), it contributed to the explanation of their abundance (deviance explained 0.74; Table 2), reaching a high abundance in warmer habitats and a lower abundance in sites where the temperature was buffered (Fig. 5). The deviance explained by the thermal regime for native taxa was lower (i.e., 0.50%), and their abundance followed a humped shaped response to the temperature with a minimum in warmer habitats (Fig. 5).

Discussion

Thermal heterogeneity in a large river floodplain

We showed that the studied floodplain covers a wide range of thermal conditions, which provides a natural system for exploring the effects of temperature on invasive species. The main river channel experiences a small range of variation between the studied sites, while the more disconnected channels covered a wider range of conditions. Permanently connected channels (i.e., eupotamal) experienced the same thermal conditions as the main river channel, due to a direct and permanent inflow from the main river channel. However, upstream disconnected channels (i.e., parapotamal) were in an intermediate situation. They receive a direct inflow of surface water from the main river channel at their downstream part, while the upstream part is disconnected and can be fed by groundwater. The more disconnected channels (plesiopotamal) exhibited the widest range of thermal conditions compared to the other channel types. These findings are similar to those that were highlighted for the braided, near-pristine Tagliamento River (Arscott et al. 2001). In the context of the Tagliamento River, authors showed that thermal regime of secondary floodplain channels can be very different from

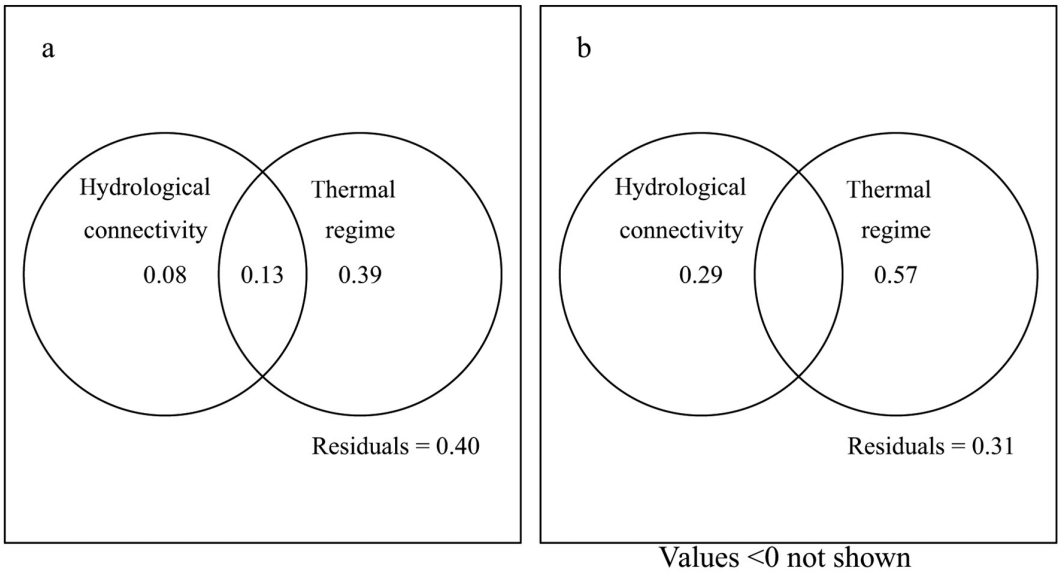


Fig. 4. Proportion of macroinvertebrate variance in the abundance matrix explained by the hydrological connectivity and thermal regime, (a) partition of variance on native taxa, (b) partition of variance on non-native species. The number between the circles indicates the interaction explained conjointly by the two sets of variables. The residuals are the information unexplained by the two sets of variables and their interaction.

each other. Similarly, Uehlinger et al. (2003) showed that the lateral heterogeneity of thermal regimes was high in a glacial floodplain. They showed that disconnected floodplain sites can have a higher average temperature throughout the year than the glacier-fed main river channel (Uehlinger et al. 2003).

The thermal regime of the floodplain channels of the Rhone River appears to be, at least in part, independent from the lateral hydrological connectivity, a major factor influencing the distribution of species at the floodplain scale (Tockner et al. 1999, Reckendorfer et al. 2006). Some isolated floodplain sites are thermally different from the main river channel and from the most connected channels, maintaining a temperature between 10°C and 12°C throughout the year (e.g., Fig. 2d). This apparent cooling during the summer and warming during winter is well documented for sites having a good vertical connectivity with the groundwater (Amoros and Bornette 2002). A major surrogate of groundwater exfiltration in the upper-Rhone floodplain channels is the water electrical conductivity (Cellot et al. 1994). The significant correlation in our results between the thermal regimes of sites with the second axis of

Table 2. Generalized additive models explaining macroinvertebrate richness and abundance by hydrological connectivity and thermal regime.

		Hydrological connectivity			Thermal regime				
Types	Groups	edf	χ^2	P	edf	χ^2	P	UBRE	Dev
Richness	Non-native	1.0	10.5	0.001**	1.0	1.1	ns	−0.05	0.51
Richness	Native	1.0	3.9	0.047*	1.8	2.3	ns	0.70	0.31
Richness	EPT	1.8	35.9	10^{-8} ***	1.3	1.6	ns	−0.03	0.79
Abundance	Non-native	2.99	904.2	10^{-16} ***	2.96	2171.1	10^{-16} ***	76.92	0.74
Abundance	Native	2.99	2775	10^{-16} ***	2.98	3227	10^{-16} ***	614.48	0.50
Abundance	EPT	2.97	1133	10^{-16} ***	2.99	1306	10^{-16} ***	363.4	0.43

Notes: edf, estimate degree of freedom; Dev, deviance explained by models; ns, non-significant; EPT, Ephemeroptera, Plecoptera, and Trichoptera.

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

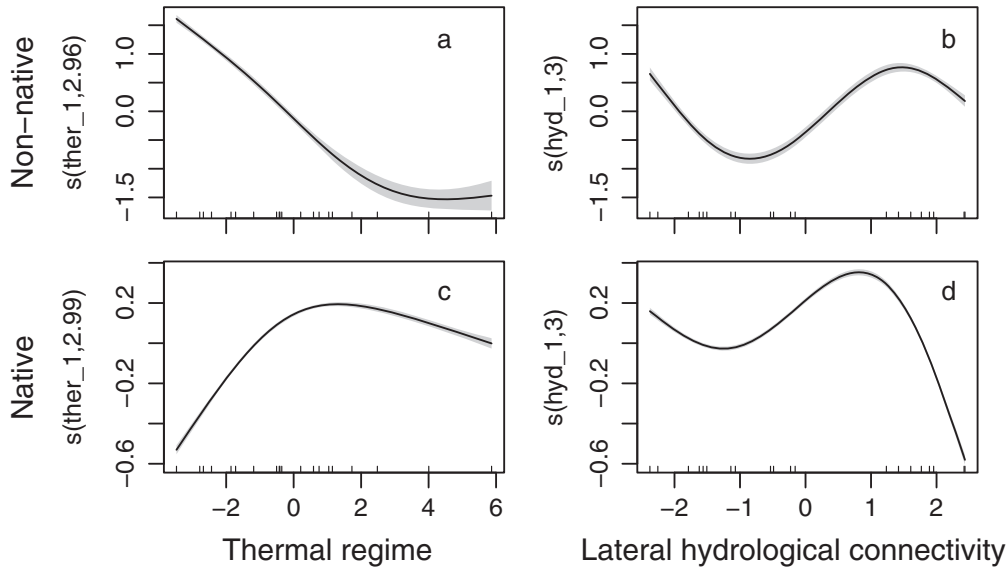


Fig. 5. Generalized additive models of non-native (a, b) and native species (c, d) density along a gradient of thermal regime from warm sites in summer (*x* axis: −2) to cold sites (*x* axis: 6), and a gradient of lateral hydrological connectivity from connected (*x* axis: −2) to disconnected sites (*x* axis: 2). The *x* values represent the scores along the first axis of principal component analysis combining variables expressing the level of lateral hydrological connectivity of the sites (Appendix S1: Fig. S6a–c) or the thermal regime of the sites (Appendix S1: Fig. S6b–d). The *y* values represent the response of non-native and native species density to the smooth of the gradient of thermal regime (ther_1) and hydrological gradient (hyd_1), with an estimated 2.99 df. Gray areas represent 95% confidence interval.

the PCA, mostly driven by conductivity, highlighted the dependence of the thermal regime with a surrogate of groundwater exfiltration. It suggests that water temperature across the Rhone floodplain is strongly influenced by exchanges with the groundwater. Other factors influencing water temperature could be the percentage of riparian shade covering the channels reducing the direct influence of solar radiation (Caissie 2006) or the more or less pronounced development of hydrophytes. The water depth of disconnected channels may also influence water temperature where stratification occurs with higher temperature at the surface and lower at the bottom. In our study, however, most of the sites had a water depth less than 2 m; therefore, vertical stratification would be unlikely.

Macroinvertebrate response to water temperature

In our study, the independence of the gradients in lateral hydrological connectivity and thermal regime allowed us to test their effects on the richness and abundance of aquatic macroinvertebrates. The gradient of hydrological connectivity seems to have a greater effect on macroinvertebrate richness than the thermal gradient. This is likely because species need to be adapted to flood disturbances in the lateral dimension of the floodplain and are therefore filtered along this gradient of hydrological connectivity (Poff 1997, Paillex et al. 2009, Gallardo et al. 2014). The thermal gradient nevertheless also showed a significant effect on the abundance of macroinvertebrates, especially non-native species density, which increased toward a maximum in the warmer sites. This observation can be related to the higher tolerance for warm habitats observed for non-native species. Indeed, Verbrugge et al. (2012) showed that the maximum temperature tolerance of native mollusks (24.0–32.0°C) was 5° lower than the tolerance of non-native species in the Rhine River. Similarly, studies using species distribution models found temperature to be a key factor in explaining the large-scale distribution of aquatic invaders (Domisch et al. 2011, Gallardo and Aldridge 2013*a*, *b*).

For native species, Milner et al. (2001) showed that the temperature in a glacier-fed stream is an important factor that drives the richness of macroinvertebrates within sites. Changes in water temperature (~2°C in the case of glacier-fed stream) can have an important effect on composition and the number of taxa per site (Milner et al. 2001). However, in an alpine glacial floodplain, hydrological connectivity was a primary factor explaining macroinvertebrate distribution while temperature had a reduced role (Burgherr et al. 2002). Studies from dry and wet Australian floodplains found temperature was not underlined as a significant factor explaining the spatio-temporal distribution of macroinvertebrates, while hydrological connectivity was (Sheldon et al. 2002, Leigh and Sheldon 2009). Similarly, macroinvertebrates in Mediterranean floodplains that can experience periodic droughts were shown to respond to changes in hydrological connectivity among floodplain channels and not necessarily to changes in temperature (Gallardo et al. 2008). Therefore, macroinvertebrates appear to be more influenced by the hydrological connectivity of a site than its thermal regime. Our results further corroborate the importance of the hydrological connectivity in explaining the distribution of taxon richness. We also find, however, that the gradient of thermal regimes is important in explaining the abundance of macroinvertebrates, especially for non-native species. While the mechanism for this apparent facilitation is unknown, we can assume that the growth rates of taxa increase with temperature and lead to denser communities in warmer sites (e.g., Brown et al. 2004). A second potential explanation could be that elevated temperatures increase productivity thus facilitating higher densities of some taxa (Brown et al. 2004). Non-native species may capitalize quicker than their native counterparts on the increase in primary productivity associated with warming temperatures, or have a superior ability to exploit local resources compared to native species, which lead to denser communities (e.g., Statzner et al. 2008). In both cases, non-native species may have considerable deleterious impacts upon native freshwater diversity through competition for habitat and resources, aggressive behavior toward native species, or transmission of pathogens affecting native populations (Gurevitch and Padilla 2004, DAISIE 2009, Gallardo et al. 2016).

Some limitations of our models should be discussed. First, results from this study refer to the Rhone river floodplain, and further studies covering a wider range of climatic and hydrological conditions are needed to generalize our results. Second, the models could be limited by the number of sites studied. However, the quality of the results and the logical shape of the responses overcome this concern. One important aspect of this success was the selection of the sites in order to cover a large range of conditions from connected to totally disconnected channels. Choosing a large river floodplain permitted to cover a large diversity of conditions and the monitoring aimed to have a series of sites well distributed along the gradient of hydrological connectivity. A third limitation concerns the unequal number of taxa included in the models. The model on native species included 185 taxa, while the model on non-native species included 12 species. The high number of native taxa included in the model could have a negative effect on its performance. Possibly, different groups of species having different levels of sensitivity to physical constraints could be mixed and reduce the level of significance of the model. One possibility would be to divide the native taxa into groups of species according to their sensitivity to physical conditions (e.g., rheophilous or lenitophilous species). Oppositely, the finer level of identification of the non-native species with relatively similar environmental preferences (mostly rheophilous species) permits to develop more robust models with a clearer response to temperature and connectivity gradients.

Future increase in water temperature in the Rhone River due to climatic change, heated effluent discharge, or greater water abstraction leading to reduced groundwater may put new pressure on native macroinvertebrates. Our findings show that sites with higher water temperatures often have higher densities of non-native species, which may in turn increase their impact on native species through increased competition for food resources and habitats, as well as alteration of food-web structure (Gallardo et al. 2016). Such modifications could impact negatively upon threatened and rare native species, which typically have a narrow range of environmental tolerance and weak competitive abilities compared to non-native species. For example, the spread of generalist top predators like

D. villosus is a threat for a wide range of native species sharing the same habitats and being target as a prey (Chapin et al. 2000, Dodd et al. 2014). This latter change is problematic as it may modify the food-web structure and the functions performed by communities at a reach scale (Chapin et al. 2000). The link between water temperature and abundance of non-native species is therefore problematic for the protection of threatened species and the functionality of aquatic communities. Within the frame of restoration measures, we recommend to diversify the level of hydrological connectivity between channels in river floodplains, in order to diversify the habitat and physical conditions. In turn, this measure will permit to maintain a high biodiversity (e.g., Reckendorfer et al. 2006, Lasne et al. 2007, Paillex et al. 2009). High level of heterogeneity could have a positive effect on maintaining sites not suitable to invasive species (Paillex et al. 2015). In turn, this could have a positive effect on the resilience of the ecosystem. Alternatively, shading river sections or deepening channels to increase vertical connectivity with groundwater could in turn buffer water temperature. Therefore, preventing waterbodies to warm-up could limit the development of dense populations of non-native species. These solutions should be tested in order to guarantee that shading or deepening a river channel has no negative side effect and ultimately limit or reduce the population of non-native species.

Conclusion

First, we showed that large river floodplains experience a wide range of thermal regimes, thereby emphasizing the importance of such environment for studies concerning the potential effect of water temperature on freshwater animal communities. Second, we showed that the thermal regime is independent from levels of hydrological connectivity between the main river channel and secondary channels, a key parameter known to influence animal community composition. Third, we showed the positive link between the water temperatures and the density of non-native species. Warm sites were found to be inhabited by abundant populations of non-native species. However, mechanisms favoring the establishment of non-native species in warmer habitats are still not elucidated. This set of empirical results based on water temperature and hydrological connectivity should aid the development of predictive models which combine key parameters for explaining the distribution of animal communities in freshwater environments. Such models would support the forecasting of the potential effects of thermal change and habitat modification on the biota of large river floodplains.

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